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Population Structure, Larval Dispersal, and Gene Flow in the Queen Conch, *Strombus gigas*, of the Caribbean

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Abstract. Genetic variation from 8 polymorphic enzyme loci among 17 population samples of queen conch, *Strombus gigas*, exhibits similarity of allelic frequencies throughout the species distribution. Analyses of standardized variances of allelic frequencies and of the frequencies of private alleles indicate that gene flow among populations in the Caribbean must be high. However, analyses of allelic frequencies clearly demonstrate that the populations are not panmictic. Bermuda is isolated from Caribbean populations, and there are numerous further examples of heterogeneity of allelic frequencies among populations within island groups. Limited data suggest that normal conch and samba, a slower growing, melanic form, are genetically differentiated.

Introduction

Gene flow, defined as the movement of gametes or individuals from one place to another and incorporation of the genetic material into the recipient population, influences both the population structure and geographic distribution of a species, as well as the adaptation of populations to their local environments (Slatkin, 1987). Gene flow is usually seen as a homogenizing force, preventing the differentiation of populations that exchange gametes or individuals (Mayr, 1963, 1970). Exchange of an average of just one individual per generation will prevent the fixation of neutral alleles arising from mutations within a population, regardless of its size (Wright, 1931). The importance of gene flow to population structure was illustrated in a comparative study of the degrees of differentiation of populations of three species of *Littorina* differing in their modes of reproduction and potential for gene flow (Berger, 1973, 1983). Larval *L. littorea* are planktonic, and hence have a high potential for gene flow. The egg cases of *L. obtusata* are attached to algae, and the algae may be detached from the substate and carried about by tides. *Littorina saxatalis* is restricted to the high intertidal and is ovoviviparous; because the eggs develop in the female until the juvenile adult stage, this species has little opportunity for gene flow. The potential for gene flow predicts the magnitude of genetic differentiation among populations. Populations of *L. littorea* are relatively homogeneous, populations of *L. saxatalis* are well differentiated, and populations of *L. obtusata* are intermediate in their degree of differentiation.

It is difficult to measure gene flow directly, so many biologists infer levels of gene flow from distances of migration or the potential for dispersal. But for several reasons these inferences can be seriously misleading. First, the movement of gametes and individuals may seriously overestimate gene flow. For example, pine pollen can be collected by ships 50 km from shore, yet studies of gene flow by pine pollen suggest that most genes move only a few dozen meters (Levin and Kerster, 1974). Pollen moving great distances may not reach receptive surfaces, or, having reached receptive surfaces, may have lost viability. Similarly, the flight of *Euphydryas* butterflies attests the potential for long distance dispersal, yet empirical studies reveal little or no gene flow among populations (Ehrlich *et al.*, 1975). Clearly, the distances that individuals can move and the distances that genes typically move can be profoundly disparate.

Second, the homogenizing effect of gene flow may be overridden by natural selection (Endler, 1973, 1977). A

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clear example has been described for the leucine aminopeptidase (Lap) polymorphism in the blue mussel, *Mytilus edulis* (Koehn and Hilbish, 1987). Mussels from estuarine and oceanic environments are differentiated at the Lap locus (Koehn *et al.*, 1976), which plays a direct role in adaptation to salinity (Koehn *et al.* 1980a; Hilbish and Koehn 1985). Populations at the eastern edge of Long Island Sound exhibit a steep cline in allelic frequency between estuarine and oceanic salinities. In the spring and early summer, tidal currents disperse planktonic larvae, obscuring the cline in allelic frequencies. Each fall, differential mortality weeds out ill-adapted genotypes, restoring the abrupt cline in frequencies (Koehn *et al.*, 1980b). A similar example can be taken from the American eel, *Anguilla rostrata* (Williams *et al.*, 1973). Although planktonic larvae from a single breeding pool are distributed by currents to the rivers of eastern North America, the environments vary from subtropical to cold temperate. Despite the redistribution of larvae each generation, several loci exhibit stable clinal variation with latitude.

Estimates of gene flow can be either direct or indirect (Slatkin, 1987). Direct methods involve tracing the dispersal of individuals, either through observation or by tagging and recapture, and subsequent estimates of reproductive success. While these methods may be applied to some species (*e.g.*, large mammals), direct methods cannot be applied to the planktonic larvae of marine organisms. Indirect methods use geographic patterns of genetic variation to infer the amount of migration that must have occurred to produce the existing pattern. Direct methods estimate the gene flow for the period of observation, but can give no indication of temporal fluctuations in gene flow through time. Indirect methods assess the cumulative effect of gene flow among populations. Consequently, indirect methods typically return higher estimates of gene flow than direct methods (Slatkin, 1987).

Here we report a study of the population structure and gene flow of a marine mesogastropod mollusk, the queen conch, *Strombus gigas* L. Laboratory studies (Ballantine and Appeldoorn, 1983; Davis and Hesse, 1983) suggest that the planktonic larvae can be dispersed by ocean currents for 12–35 days. Caribbean currents that could result in long range dispersal have typical speeds of 20–80 cm s^{-1}, but mesoscale eddies are also present that could entrain larvae and restrict their net transport (Kinder *et al.*, 1985; Lessios *et al.*, 1984). Protracted periods of larval dispersal suggest the possibility of extensive dispersal that could result in gene flow among populations in different regions of the Caribbean. In addition to describing the population structure of *S. gigas*, we have used the data on population structure to infer gene flow.

Figure 1. Collection localities for genetic studies of queen conch. 1, Bermuda; 2, Turks and Caicos Islands; 3, St. Kitts (Saint Christopher) 4, Nevis; 5, St. Lucia; 6, Bequia; 7, Grenadines; 8, Barbados; 9, Belize.

Materials and Methods

Population samples were taken throughout the range of *Strombus gigas* (Fig. 1). With the aid of fishermen and fisheries personnel, conchs were obtained by snorkeling and scuba diving. From the Atlantic we sampled the outlying populations in Oistens, Barbados, North Rock, and Bermuda. From the western Caribbean, at Ambergris Cay in Belize, we sampled both normal queen conch and the melanic morph, called samba conch. In the Turks and Caicos Is., conchs were sampled from Pine Cay, Plandon Cay, Six Hill Cay, and a samba group at French Cay. Samples were taken from the channel off Bequia, Butler's on Nevis, and at Major's Bay and Basse-Terre on St. Kitts. On St. Lucia, population samples were taken from the northern (Gros Islet) and the southern (Vieux Fort) tips of the island. Samples were collected from Saline Cay, Petit St. Vincent, and L'Esterre in the Grenadines.

At all collection localities, animals were removed from their shells and the most distal tips of the digestive glands and gonads were excised, placed in 2-cc plastic vials with screw tops, and submersed in liquid nitrogen. These samples were shipped on dry ice to the laboratory, where they were stored at −70°C. An equal volume of grinding buffer (Place and Powers, 1978) was added prior to homogenization with ultra sound. Homogenates were absorbed onto Watman #1 paper wicks and inserted into starch gels.

Variation at 18 enzyme systems was assayed with horizontal starch gel electrophoresis using a series of buffer systems. The systems most useful for resolving polymorphic loci were (1) the discontinuous lithium hydroxide

buffer, pH 8.1–8.4, of Selander *et al.* (1971), (2) the discontinuous lithium hydroxide, pH 8.5, of O'Malley *et al.* (1979), and (3) the continuous tris citrate buffer, pH 6.3–6.7, of Selander *et al.* (1971).

Seven of the 18 loci were polymorphic, and these are used here to describe the population structure of *Strombus gigas*. Their names, abbreviations, and the buffer systems used to resolve them are as follows: 6-phosphogluconate dehydrogenase, 6Pgd, buffer 3; phosphoglucomutase, Pgm-1, buffer 2; phosphoglucomutase, Pgm-2, buffer 1; glycerate dehydrogenase, Gdh, buffer 2; aminopeptidase, Ap, buffer 1; leucine aminopeptidase, Lap, buffer 2; malate dehydrogenase, Mdh, buffer 3. Alleles were numbered by electrophoretic mobility, with the fastest migrating allele designated "1."

Our stain for phosphoglucomutase is similar to that of Shaw and Prasad (1970) except that we used a form of glucose-6-phosphate dehydrogenase that is more active with NAD than with NADP (Sigma G 5760). Pgm-1 stained quite well with only NAD, but Pgm-2 had insufficient activity with NAD, and good activity with NADP. Our stain for glycerate dehydrogenase was the same as any other NAD-dependent dehydrogenase, but the substrate solution was made as follows: 0.2 g glyceric acid plus 0.5 g L-histidine dissolved in 50 ml water, adjusted to pH 9.0 with 1 *M* NAOH.

Heterogeneity of allelic frequencies was tested as in Workman and Niswander (1970). F_{st}, a standardized measure of variation in allelic frequencies, was calculated as

$$F_{st} = S^2/p(1 - p) \quad (1)$$

where S^2 is the observed variance in allelic frequencies among localities, and p is the mean allelic frequency. Nm, the product of population size and migration rate, is estimated, following Slatkin (1985a, b, 1987), as

$$Nm = (1/F_{st} - 1)/4 \quad (2)$$

Thus, genetic variation at each polymorphic locus is used to estimate the number of individuals exchanged between populations each generation.

Results

Macrogeographic variation

Two alleles were segregating at Pgm-1, Ap, and Mdh. A rare (0.03) fast allele was found at 6Pgd, but only at Gros Islet on St. Lucia. A slow allele at Pgm-2 was found at Bermuda and Barbados, but these alleles appeared in single heterozygotes. Four alleles were detected at Gdh. At all localities the slow allele was most common, and in some localities, it was the only allele present. A single very slow allele was detected at Basse-Terre, St. Kitts; this allele was not found at other localities. The fast and medium alleles had similar mobilities, and their similarity, in combination with the low activity of this locus, made it difficult to differentiate these alleles. For a conservative estimate of differentiation of populations, the fast and medium alleles at Gdh were pooled (Table I). A rare, slow allele at the Ap locus appeared in one individual from Barbados, but nowhere else. Allelic frequencies for the 7 polymorphic loci in 17 population samples are summarized in Table I.

Although the differentiation of allelic frequencies among populations is generally statistically significant, most populations are quite similar. For example, the same allele is generally the most abundant at all collection localities (minor exceptions are 6Pgdh and Ap at Vieux Fort, St. Lucia, and Ap at Bermuda). Thus, a first impression from Table I is of general genetic similarity of populations throughout the range of *Strombus gigas*.

Gene flow

In addition to the allelic frequencies, F_{st} and the derived estimate of Nm for each locus are also presented in Table I. Values of Nm for 6Pgd, Pgm-1, Pgm-2, Gdh, Ap, Lap, and Mdh are 6.4, 11.5, 19.0, 2.9, 12.9, 1.5, and 0.9, respectively. The geographic distribution of genetic variation at Mdh is patchy, for there is a substantial level of genetic variation in Bermuda, but little variation within the Caribbean. If Bermuda is dropped from this analysis, the value of Nm for Mdh jumps to 6.8. The disparity in these estimates suggests that Bermuda is isolated from populations in the Caribbean. Using the second estimate, the mean value for Nm is 8.7.

Private alleles, defined as allelic variants restricted to single populations (Neel, 1973), may be used to estimate Nm using the formula of Slatkin (1985a):

$$\ln (p) = -.505 * \ln (Nm) - 2.44 \quad (3)$$

in which p is the average frequency of private alleles, N is population size, and m is the migration rate. Three alleles appear to be candidates for private alleles. A very fast allele at 6Pgd reaches a frequency of 0.051 in Gros Islet, St. Lucia, a very slow allele at Gdh has a frequency of 0.01 in Basse-Terre, St. Kitts, and a very slow allele at Ap has a frequency of .018 at Oistens, Barbados. When the mean of these frequencies (.026) is used in Equation 3, the estimate of Nm is 11.0. Both this estimate and the estimate derived from Equation 2 (Nm = 8.7) suggest that gene flow is or has been relatively high throughout the range of this species.

Allelic frequencies in Bermuda are representative of the Caribbean populations for 6Pgd, Pgm-1, Pgm-2, Ap, and Gdh. But the allelic frequencies of Lap and Mdh are both outside the range seen in the Caribbean (Table I). For example, the frequency of the fast allele is .30 in Ber-

Table I

Allelic frequencies, Fst and Nm, in queen conch

		6Pgd			Pgm-1		Pgm-2			Gdh			Ap			Lap		Mdh	
Locality allele	n	1	2	3	1	2	1	2	3	1+2	3	4	1	2	3	1	2	1	2
Bermuda	41	.00	.25	.75	.23	.77	.31	.68	.01	.28	.72	.00	.51	.49	.00	.38	.62	.30	.70
Turks & Caicos																			
Pine Cay	56	.00	.28	.72	.44	.56	.40	.60	.00	.28	.72	.00	.47	.53	.00	—	—	.00	1.00
French Cay	53	.00	.36	.64	.28	.72	.31	.69	.00	.16	.84	.00	.44	.56	.00	—	—	.00	1.00
Plandon Cay	40	.00	.28	.72	.35	.65	—	—	—	.23	.77	.00	.39	.61	.00	—	—	.00	1.00
Six Hill Cay	25	.00	.30	.70	.20	.80	—	—	—	.30	.70	.00	.23	.77	.00	.06	.94	—	—
St. Kitts																			
Major's Bay	31	.00	.42	.58	.35	.65	.35	.65	.00	.04	.96	.00	.42	.58	.00	.00	1.00	—	—
Basse-Terre	48	.00	.25	.75	.35	.65	—	—	—	.04	.95	.01	—	—	—	.23	.77	—	—
Nevis	48	.00	.29	.71	.32	.68	.32	.68	.00	.19	.81	.00	.46	.54	.00	—	—	—	—
St. Lucia																			
Gros Islet	71	.03	.31	.66	.42	.58	.47	.57	.00	.34	.66	.00	.44	.56	.00	.23	.77	.04	.96
Vieux Fort	48	.00	.51	.49	.39	.61	.32	.68	.00	.00	1.00	.00	.52	.48	.00	.31	.69	.02	.98
Bequia	29	.00	.21	.79	—	—	.36	.64	.00	—	—	—	.38	.62	.00	—	—	.00	1.00
Grenadines																			
Petit St. Vincent	47	.00	.33	.67	.24	.76	—	—	—	—	—	—	.48	.52	.00	.25	.75	.00	1.00
Saline Cay	63	.00	.33	.67	.33	.67	—	—	—	.02	.98	.00	.42	.58	.00	.24	.76	.00	1.00
L'Esterre	40	.00	.21	.79	.38	.62	—	—	—	.17	.83	.00	.41	.59	.00	—	—	.00	1.00
Barbados	27	.00	.30	.70	.29	.71	.31	.68	.01	.40	.60	.00	.48	.50	.02	—	—	.05	.95
Belize																			
(normal)	24	.00	.28	.72	.27	.73	—	—	—	.17	.83	.00	.44	.56	.00	.00	1.00	.00	1.00
(samba)	23	.00	.32	.68	.33	.67	—	—	—	.24	.76	.00	.49	.51	.00	.00	1.00	.00	1.00
Mean allelic frequency		.00	.31	.69	.32	.68	.35	.65	.00	.19	.81	.00	.44	.56	.00	.17	.83	.03	.97
F_{st}			.038		.021		.013			.080			.019			.142		.220	
Nm			6.4		11.5		19.0			2.9			12.9			1.5		0.9 (6.8)	

Note: — indicates missing data. Value in parentheses for Nm was calculated excluding Bermuda. Alleles are listed in decreasing eletrophoretic mobility.

muda, but this allele is not seen in most of the Caribbean populations, and where it is found it does not have frequencies higher than 0.05. Once again, these data suggest that Bermuda is isolated from the Caribbean populations.

Microgeographic variation

Although gene frequencies at most loci do not differ strikingly among populations, and the estimate of gene flow is estimated to be relatively high, allelic frequencies at some loci are heterogeneous among population samples taken within island groups (Table II). For example, St. Lucia is a small, oval island, and although Gros Islet and Vieux Fort are localities at opposite ends of the island, they are only 40 km apart. Despite this geographic proximity, the population samples from these localities were significantly differentiated for 6Pgd, Pgm-2, and Gdh. Similarly, Pgm-1 and Ap allelic frequencies were heterogeneous in the Turks and Caicos, and 6Pgd, Gdh, and Lap allelic frequencies were heterogeneous in St. Kitts and Nevis. In the Grenadines, allelic frequencies at Gdh were heterogeneous. Thus, there are numerous examples of microgeographic variation within island groups.

Samba

In Belize, we collected samples of both normal conch and samba, a smaller, melanic form that is generally shunned by fishermen because of its size and dark meat. Allelic frequencies are similar for these samples for all loci except Gdh. Table I presents the sum of alleles 1 and 2, but the frequencies of these alleles differ between the

Table II

Tests of homogeneity of allelic frequencies within island groups in queen conch

Area	Locality	6Pgd	Pgm-1	Pgm-2	Gdh	Ap	Lap	Mdh
Turks and Caicos	Pine Cay French Cay Plandon Cay Six Hill Cay	NS	*	NS	NS	*	—	NS
St. Kitts and Nevis	Basse-Terre Major's Bay Butlers	*	NS	NS	**	NS	**	—
St. Lucia	Gros Islet Vieux Fort	**	NS	*	***	NS	NS	NS
Grenadines	Petit St. Vincent Saline Cay L'Esterre	NS	NS	—	***	NS	NS	—

Note: — indicates missing data. *= $P < .05$, **= $P < .01$, ***= $P < .001$.

morphs. For samba, the frequencies (and standard errors) of alleles 1, 2, and 3 are 0.22 (0.06), 0.02 (0.02), and 0.76 (0.06), while the corresponding frequencies for the normal conch are 0.00, 0.17 (.05), and 0.83 (0.05). The samba and the normal conch do not appear to be random samples from a randomly mating population ($P < 0.01$). We also sampled samba from French Cay, but all of the mature animals obtained were samba, so we could not replicate the comparison of normal and samba conch from Belize. Samples from other localities in the Turks and Caicos contain only normal conchs. There are differences between French Cay and the other Cays in the Turks and Caicos, especially at Gdh and 6Pgd, but these might be attributable to microgeographic variation rather than differentiation of normal and samba conch.

Discussion

Marine molluscs with planktonic larvae are known for their capacity to disperse, yet their effective range of dispersal may be much more limited than their presence in the plankton implies (Scheltema, 1971). Transoceanic dispersal of larvae has been suggested (Scheltema, 1971, 1972, 1978, 1986a, b; Pechenik *et al.*, 1984; Scheltema and Williams, 1983), but the crucial question—whether significant proportions of the larvae found in the middle of the ocean are capable of metamorphosis and survival, and contribute significantly to down-stream gene pools—has not been answered (Laursen, 1981). Unfortunately, studies of gene flow have not been carried out on teleplanic species. The advent of biochemical genetic techniques and modern statistical methods (*e.g.*, Slatkin, 1985a, b) now makes this possible.

Larvae attributed to the genus *Strombus* have been collected from both nearshore (Berg, 1975, 1976, and unpub. data) and oceanic waters (Laursen, 1981; Scheltema, pers. comm.) of the Atlantic and Pacific oceans. The effective duration of larval life under normal planktonic conditions is unknown. D'Asaro (1970) reared *S. gigas* larvae for 60 to 75 days on natural phytoplankton supplemented with laboratory reared species, but no conch metamorphosed and it is not known if the larvae were competent to do so. Repeated rearings of extensive numbers of larvae in laboratories throughout the Caribbean have shown that metamorphosis occurs between 12 days (Ballantine and Appledoorn, 1983) and 35 days (Davis and Hesse, 1983), with an average duration of 21 days. Thus, larvae of *S. gigas* have the potential to be transported throughout the Caribbean. Extensive gene flow throughout the Caribbean is consistent with the similarity of allelic frequencies in that region (Table I).

Estimates of Nm derived from F_{st} and from the frequency of private alleles are concordant, and they are also in agreement with predictions based on the life history of this species. The extended larval stage provides the potential for long distance dispersal, and the population structure of *S. gigas* indicates either that dispersal among localities is relatively common (on the order of 10 individuals exchanged among localities per generation), or was so in the recent past.

Although extensive gene flow is suggested, conchs are certainly not a single randomly mating population, for there are clear discontinuities in allelic frequencies. For example, Bermuda appears to be isolated from the populations in the Caribbean. Currents from the Caribbean and Gulf of Mexico sweep past the Florida Keys as the Florida Current and then north along the Atlantic coast as the Gulf Stream, passing far west of Bermuda in an arc northeastward to form the North Atlantic drift. Gulf Stream rings occasionally approach Bermuda (Robinson, 1983; Hogg *et al.*, 1978) bearing other teleplanic lar-

vae (Scheltema, 1986b), but it is not known if they carry *Strombus* larvae. As might be predicted, decimated conch stocks in Bermuda have not recovered despite 10 years of protection. Abbott and Jensen (1967) report cyclic disappearances of species in shell collections from Bermuda over the previous 110 years, including the congeneric *S. costatus*, which has a larval period similar to that of *S. gigas* (Brownell, 1977; Ballantine and Appeldoorn, 1983). Although *Strombus alatus* is the most common species of *Strombus* in northern areas and its planktonic larvae occur in the neritic waters off North Carolina (Thiriot-Quievreux 1983), it disappeared from Bermuda sometime since the Pleistocene, when glaciers forced the Gulf Stream to the south and into a more east-west orientation, bringing it closer to Bermuda (Keffer *et al.*, 1988). Bermuda now lies in the central oceanic gyre of the North Atlantic, more than 1500 km from the Gulf Stream. It is doubtful that viable larvae of the genus *Strombus* are ever carried to Bermuda and therefore the population in Bermuda must be self sustaining. The same may be true for the upstream population on Barbados that exhibits rare slow alleles at Pgm-2 and Ap. The population around Barbados was decimated in the 1930's and has never regained its previous size. Consequently, traditional recipes for its cooking have been lost to native cooks. Animals are breeding around both of these islands (Berg, pers. obs.), and retention of their offspring in local circulations (Farmer and Berg, in press) may be sufficient to maintain the populations at low densities.

Unlike Bermuda and Barbados, the Turks and Caicos Islands, Cuba, and the Bahamas are all downstream of the eastern Caribbean conch populations and appear to experience high annual recruitment. These populations support large fisheries, but even when decimated by over fishing they recover quickly if management measures are followed (Munoz *et al.*, 1987; Berg, pers. obs.).

Variation among islands within archipelagos is apparent in our samples taken from the Turks and Caicos, St. Kitts and Nevis, St. Lucia, and the Grenadines. St. Lucia is an elipse with a long axis (north-south) perpendicular to prevailing winds and strong ocean currents (Kinder *et al.*, 1985). Despite the close proximity of Gros Islet and Vieux Fort, and the lack of obvious differences in habitat or gross morphology of *S. gigas* from these two areas, their populations are significantly differentiated. A possible explanation may be that the east-west currents prohibit exchange of larvae between these localities; mixing of larvae may occur far in the lee of islands, but not near shore. Eddies formed in the lee of islands (Emery, 1972) and current reversals (Mazeika *et al.*, 1983) could retain larvae and allow differentiation in these upstream areas, while downstream populations may receive larvae from many sources. Complex currents may restrict gene flow among localities in close proximity in other areas of the Caribbean.

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